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Gyrodactylus rafinesqueii sp. n. (Monogenea) from *Etheostoma rafinesquei* (Percidae) in Kentucky, with a Review of the Taxonomy and Host Specificity of Species of *Gyrodactylus* from Etheostomatid Fishes in North America

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ABSTRACT: *Gyrodactylus rafinesqueii* sp. n. (Monogenea) is described from the trunk surfaces, fins, and gonopodium of the Kentucky snubnose darter (*Etheostoma rafinesquei*) from Russell Creek, Kentucky. The species has moderately sized hamuli (56–65 μm long), a ventral bar with prominent (14–18 μm long) anterolateral processes and a tapered membrane, and a relatively large, slender marginal hook sickle (8.0–8.5 μm long). An illustrated comparison of the sclerites of *G. rafinesqueii* sp. n. to those of related species known from etheostomatid fishes (*G. bretinae* Wellborn, 1967; *G. etheostomae* Wellborn and Rogers, 1967; *G. nigrum* Rogers, 1975; *G. percinae* Rogers and Wellborn, 1965) is presented. *Gyrodactylus rafinesqueii* sp. n. resembles most closely *G. percinae* but has larger marginal hook sickles and a dorsal bar devoid of a distinct medial notch. Within various rivers studied in Kentucky, *G. rafinesqueii* sp. n. parasitized *E. rafinesquei*, *E. flavum*, and *E. simoterum*, all three of which are species of darters classified in the subgenus *Nanostoma/Ulocentra*. *Gyrodactylus rafinesqueii* sp. n. did not parasitize species of darter of other subgenera living syntopically in the same habitat. In contrast, *G. etheostomae* parasitized hosts (*E. barrenense*, *E. caeruleum*, *E. spectabile*, and *E. stigmaeum*) of 3 subgenera and thus has a much broader host specificity. Field collections revealed that *G. rafinesqueii* sp. n. and *G. etheostomae* can co-occur within the same stretch of river but that they do not share hosts. Both apparently are dependent on darters, for neither parasite was found on cyprinid fishes sampled at the same sites. A key to species of *Gyrodactylus* from etheostomatid fishes and preliminary thoughts on the evolutionary history of gyrodactylids on these fishes are included.

KEY WORDS: Monogenea, *Gyrodactylus rafinesqueii*, *Gyrodactylus etheostomae*, darter fishes, Kentucky, North America.

Four species of *Gyrodactylus* Nordmann, 1832, have been described from the body surfaces and fins of etheostomatid fishes in North America. They are *G. percinae* Rogers and Wellborn, 1965, from the blackbanded darter (*Percina nigrofasciata*) in Alabama (Rogers and Wellborn, 1965); *G. bretinae* Wellborn, 1967, from the speckled darter (*Etheostoma stigmaeum*) in Arkansas (Wellborn, 1967), *G. nigrum* Rogers, 1975, from the johnny darter (*E. nigrum*) in Alabama, and *G. etheostomae* Wellborn and Rogers, 1967, from the orangebelly darter (*E. radiosum*) in Arkansas (Wellborn and Rogers, 1967), the mud darter (*E. asprigene*) in North Dakota (Kritsky and Leiby, 1971), the Iowa darter (*E. exile*) in Ontario (Molnar et al., 1974), the rainbow darter (*E. caeruleum*) in Kentucky (Kozel and Whittaker, 1982), and the johnny darter, (*E. nigrum*) in Lake Ontario (Hanek and Fernando, 1971; Dechtiar and Christie, 1988) and in Lake Huron (Dechtiar et al., 1988).

The present study describes *Gyrodactylus rafinesqueii* sp. n. from the Kentucky snubnose darter (*E. rafinesquei*) and examines the host specificity of the parasite among species of darters living syntopically at selected sites in Kentucky streams. The study compares taxonomically *G. rafinesqueii* sp. n. and the preceding species.

Materials and Methods

Parasites studied originated from host fishes sampled from stream sites in 7 Kentucky counties and 2 drainage basins: 3 and 13 April 1992, Brush Creek, Green County; 21 February 1992, Marrowbone Creek, Cumberland County; 9 December 1992 and 15 April 1993, Middle Pitman Creek, Taylor County; and 9 and 17 April 1993, Russell Creek, Adair County; 27 December 1994, Trammel Fork of Drakes Creek, Allen County; 28 December 1994, Whipporwill Creek of Red River, Logan County, and Elk Fork of Red River, Todd County (Fig. 1). Sites 1, 2, and 4 (Fig. 1) were in the Cumberland River Drainage. Sites 3 and 5–7 were in the Green River Drainage. At Sites 4, 6, and

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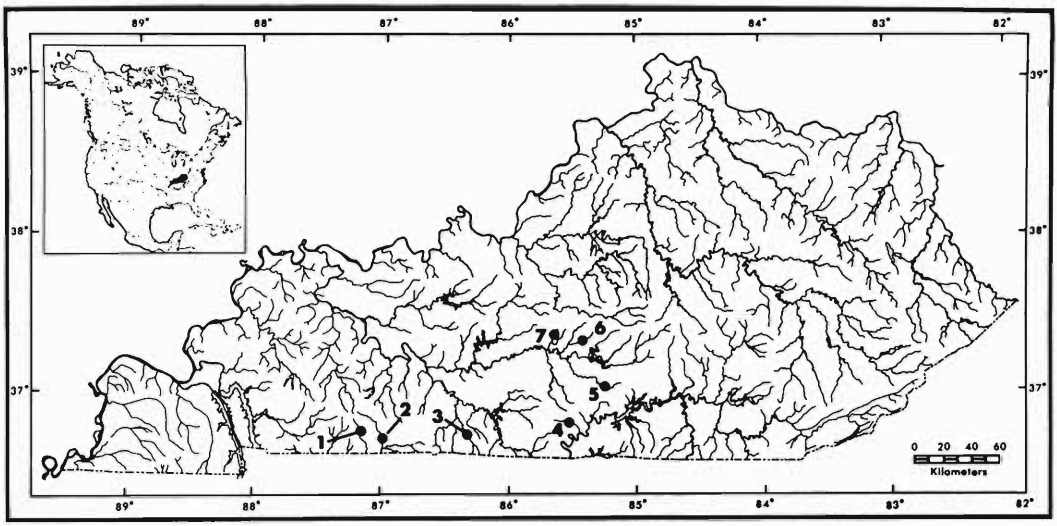


Figure 1. Map of Kentucky showing the location of 7 sampling sites. Site 1, Elk Fork, Todd County, 87°07′27″W, 36°44′02″N. Site 2, Whipporwill Creek, Logan County, 86°58′54″W, 36°45′41″N. Site 3, Trammel Fork, Allen County, 86°16′16″W, 36°44′23″N. Site 4, Marrowbone Creek, Cumberland County, 85°32′46″W, 36°50′37″N. Site 5, Russell Creek, Adair County, 85°10′53″W, 37°03′18″N. Site 6, Middle Pitman Creek, Taylor County, 85°24′04″W, 37°22′20″N. Site 7, Brush Creek, Green County, 85°35′46″W, 37°24′15″N. Modified with permission from Burr, B. M., and M. L. Warren, Jr. 1968. A distributional atlas of Kentucky fishes. Ky. Nature Preserves Comm., Sci. and Tech. Series A, 398 pp.

7 (Fig. 1), fish were preserved in 10% formalin. The sampling at Russell Creek (Site 5, Fig. 1) was much more extensive. Fishes were collected for about 6 hr using various-sized seines. Each species of fish captured was kept in a separate bag until 10–15 individuals were obtained. The fish were then placed in jars with a 1:4,000 formalin solution. The parasites were allowed to settle and then pipetted into small jars containing 5% formalin; the fish were removed and fixed in 10% formalin. The same protocol was followed at Sites 1–3 (Fig. 1), but collections were limited to darters.

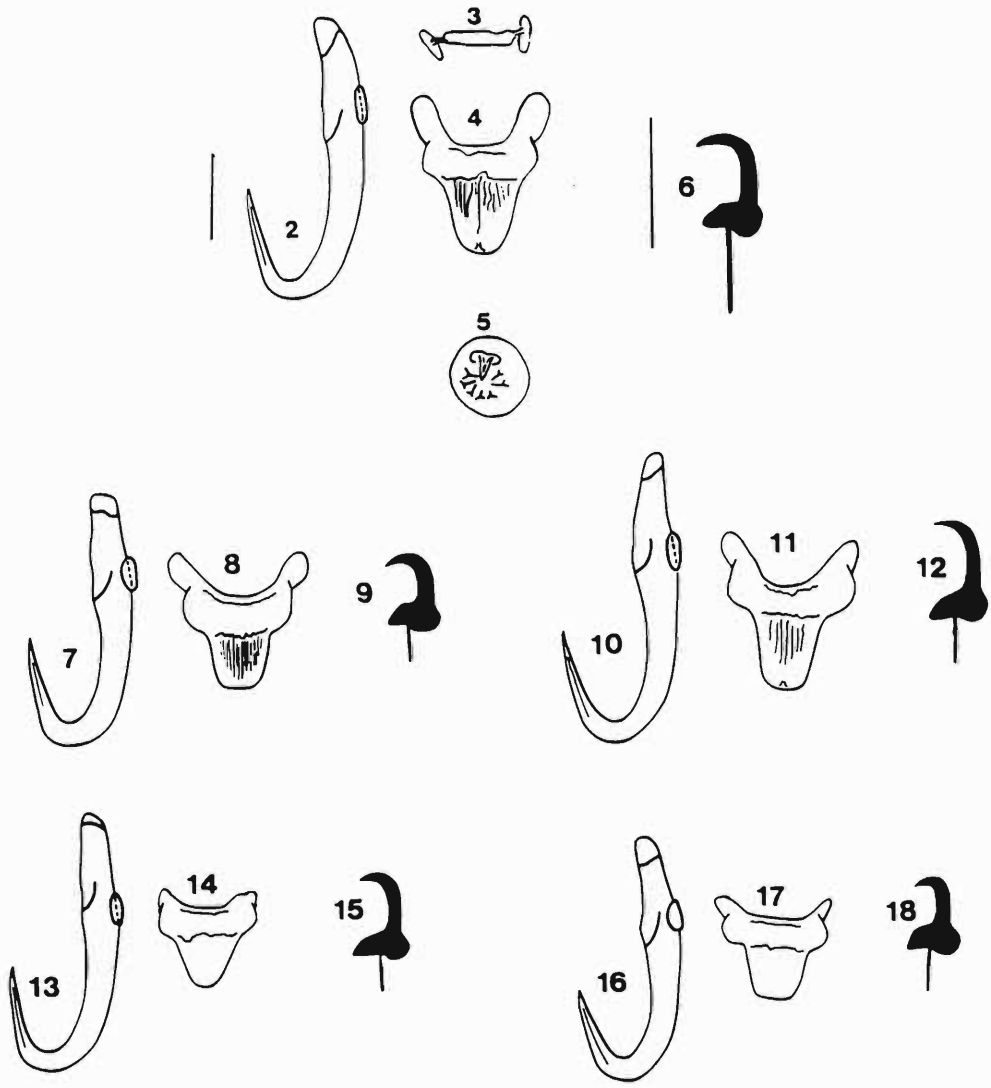
Preserved parasites were mounted unstained in a 50% solution of glycerine–water and allowed to clear for over 1 yr. Cleared specimens were studied microscopically and relevant morphometric features were determined from drawings prepared by means of an optical drawing tube. Photographs of the marginal hooks were used as an important reference when preparing the final drawings of the marginal hook sickles. Permanent slides were prepared by soaking the slide overnight in tapwater and then removing the coverslip. The specimen (which usually remained adhered to either the slide or the coverslip) was dehydrated in a graded ethanol series, cleared in xylene, and mounted in Canada balsam. Unless stated otherwise, all measurements are presented in micrometers. Those of the holotype are followed in parentheses by the mean, ±1 standard deviation, range, and number of measurements determined for of those of the paratypes.

Type and voucher specimens of 4 species of *Gyrodactylus* housed in the United States National Parasite Collection (USNPC), Beltsville, Maryland, were examined. These included *G. bretinae* (holotype USNPC 61626 and paratype USNPC 61627), *G. etheostomae* (holotype USNPC 60879, paratype USNPC 60880, and a voucher specimen USNPC 71659), *G. nigrum* (holotype USNPC 71232 and paratype USNPC 71233), and *G. percinae* (holotype USNPC 61027).

Results

Gyrodactylus rafinesqueii sp. n. (Figs. 2–6)

DESCRIPTION: Flattened specimen 460 (mean = 410, ± 61 [SD], range = 320–460, n = 8) long, 95 (86, ±6.5, 80–95, n = 8) wide at midbody. Pharynx 33 (29, ±3.1, 26–33, n = 4) long, 21 (25.5, ±3.8, 21–30, n = 4) wide. Penis 13 (13.4, ±0.7, 13–14, n = 2) in diameter, with 1 large spine and a row of 6 small spines. Developing embryo encased within thin-walled, stretchable, bipolar "shell." Hamuli 60 (61.2, ±2.7, 56–65, n = 9) long; root 23 (19.6, ±2.5, 16–23, n = 9), shaft 42 (43, ±1.7, 41–46, n = 9), point 24 (25.6, ±2.0, 23–28, n = 9). Ventral bar 8 (6.2, ±0.8, 5–8, n = 10) long, 23 (24.6, ±1.6, 22–26, n = 10) wide, with anterolateral processes 10 (10.8, ±0.9, 14–18, n = 10) long. Ventral bar membrane 18 (16.2, ±1.1, 14–18, n = 10) long. Dorsal bar tubular. Marginal hook 28.5 (29.5, ±1.8, 27–32, n = 6) long; sickle 8.5



Figures 2–18. Taxonomically important features of species of *Gyrodactylus* Nordmann, 1832 (Monogenea), known from darter fishes of North America. All structures except the marginal hook sickles are drawn to the same scale, bar = 20μm. Marginal hook sickles are all drawn to the scale of the bar = 10 μm. 2–6. *Gyrodactylus rafinesqueii* sp. n. on the body surface of *Etheostoma rafinesquei*. 2. Sclerotized hamulus (holotype USNPC). 3. Dorsal bar (voucher specimen). 4. Ventral bar (holotype USNPC). 5. Penis (holotype USNPC). 6. Lateral view of marginal hook (holotype USNPC 86709). 7–9. *Gyrodactylus percinae* Rogers and Wellborn, 1965. 7. Hamulus (holotype USNPC 61027). 8. Ventral bar (holotype USNPC 61027). 9. Marginal hook sickle (holotype USNPC 61027). 10–12. *Gyrodactylus bretinae* Wellborn, 1967. 10. Hamulus (paratype USNPC 61627). 11. Ventral bar (paratype USNPC 61627). 12. (paratype USNPC 61627). 13–15. *Gyrodactylus nigrum* Rogers, 1975. 13. Hamulus (paratype USNPC 71233). 14. Ventral bar (paratype USNPC 71233). 15. Marginal hook (paratype USNPC 71233). 16–18. *Gyrodactylus etheostomae* Wellborn and Rogers, 1967. 16. Hamulus (paratype USNPC 60880). 17. Ventral bar (paratype USNPC 60880). 18. Marginal hook sickle (paratype USNPC 60880).

(8.1, ±0.2, 8.0–8.5, n = 7) long, 4.0 (4.3, ±0.2, 4.0–4.5, n = 7) wide proximally, 5.5 (4.7, ±0.5, 4.0–5.5, n = 7) wide distally; handle 21.5 (21.9, ±1.6, 20–24.5, n = 6) long; filament 8.5 (8.5, ±0.0, n = 5) long.

TYPE HOST: Kentucky snubnose darter (*Etheostoma rafinesquei* Burr and Page, 1982) (Percidae; Etheostomatini). Other known hosts include the Tennessee snubnose darter (*E. simoterum*) and the saffron darter (*E. flavum*).

SITES ON HOST: Principally, the base and membranes of fins and the gonopodium of females.

TYPE LOCALITY: Holotype and paratype specimens from Middle Pitman Creek, Kentucky Highway 210 (85°24′04″W, 37°22′20″N), Taylor County, Kentucky 15 April 1993). Other specimens studied were from Russell Creek, Adair County (January and April 1993), and Brush Creek, Green County (April 1992), both in Kentucky.

SPECIMENS STUDIED: Ten. Holotype and paratype specimens are deposited in the USNPC No. 86709, Beltsville, Maryland.

PREVALENCE AND INTENSITY OF INFECTION: As part of another study on the ecology of *E. rafinesquei* in Middle Pitman Creek, Kentucky, the prevalence and intensity of *G. rafinesqueii* sp. n. was noted on monthly samples collected from August 1987 to July 1988. Parasites were absent or rare in the months of May to October. However, the parasite was relatively common from November to April, with prevalence being 86% (n = 36 examined) in winter (December to February) and 91% (n = 33 examined) in spring (March to May). Mean intensity was the greatest during winter and spring at 13.2 and 10 parasites, respectively.

HOST SPECIFICITY: At Russell Creek, *G. rafinesqueii* sp. n., *G. etheostomae*, and *G. campostoma* Wellborn, 1967, were collected. The results reveal that, in spite of co-existing in the same stream reach, *G. rafinesqueii* sp. n. parasitized only *E. rafinesquei* whereas *G. etheostomae* parasitized *E. caeruleum* and *E. stigmaeum*. *Gyrodactylus campostoma* parasitized only *Campostoma oligolepis*. Seven species of fish at the site, including 3 darters (22 *E. bellum*, 9 *E. blennioides*, and 8 *E. flabellum*) and 4 cyprinids (2 *Cyprinella spilopterus*, 32 *Luxilus chrysocephalus*, 16 *Lythrurus ardens*, and 17 *Pimephales notatus*), were devoid of the parasites.

At Middle Pitman Creek, *G. rafinesqueii* sp. n. occurred only on *E. rafinesquei*, whereas *G. etheostomae* occurred on *E. caeruleum* and *E. spectabile*.

At Marrowbone Creek, *G. rafinesqueii* sp. n. parasitized *E. simoterum*. Gyrodactylid parasites were not found on the darters *E. blennioides*, *E. rufilineatum*, and *E. spectabile* nor on the cyprinids *Notropis telescopis* and *N. boops*.

At Whipporwill Creek, *G. rafinesqueii* sp. n. parasitized *E. simoterum* and *E. flavum*.

At Trammel Fork, *G. etheostomae* parasitized *E. caeruleum* and *E. barrenense*.

At Brush Creek, *G. rafinesqueii* sp. n. parasitized *E. rafinesquie* whereas *G. etheostomae* parasitized *E. caeruleum*.

At Elk Creek, *G. rafinesqueii* sp. n. parasitized *E. flavum*.

ETYMOLOGY: This species is named after the host on which it was first collected.

COMMENTS: *Gyrodactylus rafinesqueii* sp. n. resembles most closely *G. percinae* Rogers and Wellborn, 1965, a species described from the fins and body surface of the blackbanded darter (*P. nigrofasciata*) from Moore's Mill Creek, Lee County, Alabama. Both species are of medium body size for gyrodactylids and have similarly shaped hamuli (Figs. 2, 7). The ventral bar has prominent anterolateral projections and a similarly proportioned membrane (Figs. 4, 8). However, *G. rafinesqueii* sp. n. has relatively large sickles compared to those of *G. percinae* (Figs. 6, 9) and does not possess a medial notch in the dorsal bar, a feature that is considered diagnostic for *G. percinae* (Rogers and Wellborn, 1965).

Discussion

During the present study, we examined type material of *G. bretinae*, *G. etheostomae*, *G. nigrum*, and *G. percinae*. We concluded that all 4 represent valid taxa but that existing descriptions are lacking in taxonomically important details of the hamulus and/or the marginal hook sickle. To help address this problem, we provide a detailed comparison of *G. rafinesqueii* sp. n. with these related species.

Gyrodactylus percinae was described from the fins and body of the blackbanded darter (*Percina nigrofasciata*) in Moore's Mill Creek, Alabama (Rogers and Wellborn, 1965), but has not been reported in any subsequent parasite surveys. Study of the type material revealed that the original species description is accurate. Important diagnostic features include the relatively

short, robust hamuli (Fig. 7) and a ventral bar with distinct anterolateral projections and a blunt membrane (Fig. 8). We supplement the description by providing important details on the size and shape of the marginal hook sickle (Fig. 9).

Gyrodactylus bretinae was described from the fins and body of the speckled darter (*E. stigmaeum*) at the National Fish Hatchery, Corning, Arkansas (Wellborn, 1967). This species has also not been reported in surveys published since the description. We examined the holotype and paratype specimens and, in spite of the specimens having dried significantly since deposition, the sclerites are visible in lateral view. We concur with Wellborn's (1967) description with respect to the size and depicted shapes of the ventral and dorsal bars and the penis and its terminal spines. The hamulus as it is originally described is slightly exaggerated in overall thickness, our interpretation of these sclerites of the types being that they are thinner (Fig. 10). Furthermore, as originally described, the sickle of the marginal hook is also too thick. The ventral bar has distinct anterolateral processes (Fig. 11). The type specimens reveal that the shaft and point of the sickle are very slender (Fig. 12).

Gyrodactylus nigrum (Figs. 13–15) was described from johnny darter (*E. nigrum*) in Cubahatchee Creek, Alabama (Rogers, 1975). As with *G. percinae* and *G. bretinae*, it has not been reported subsequently in the literature. However, we believe the species identified as *G. etheostomae* from johnny darter in the Bay of Quinte, Lake Ontario, by Hanek and Fernando (1971) was in fact *G. nigrum*. We believe this because our study of the type specimens showed that *G. nigrum* has marginal hooks with a relatively long, slender sickle (Fig. 15) not depicted accurately in the original species description. Drawings provided by Hanek and Fernando (1971) of specimens collected from johnny darter and identified as *G. etheostomae* show long, thin sickles characteristic of *G. nigrum* (Fig. 15).

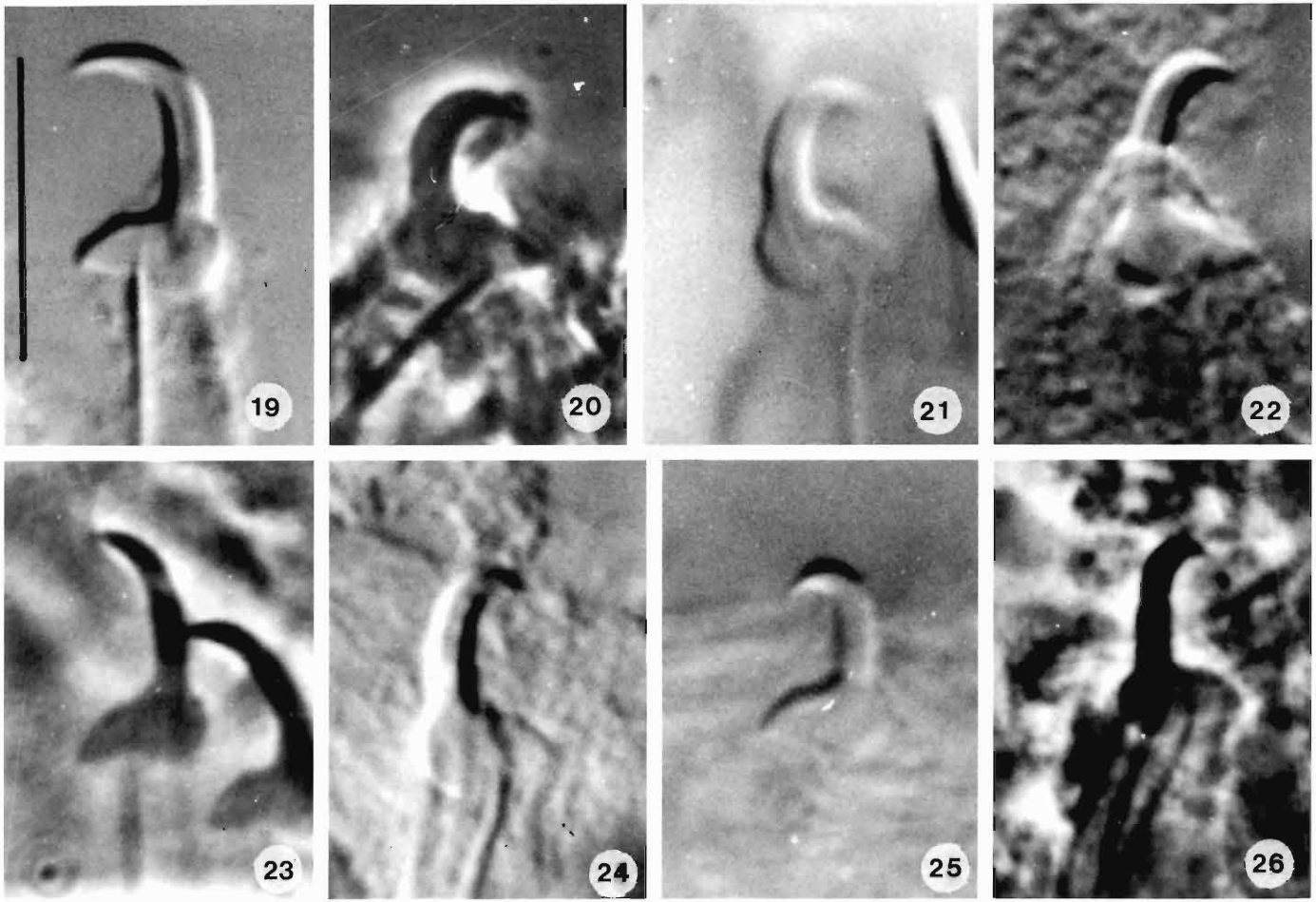
Gyrodactylus etheostomae is the most commonly reported species of *Gyrodactylus* from etheostomatid fishes. It was originally described from the orangebelly darter (*G. radiosum*) in Mammoth Spring, Arkansas (Wellborn and Rogers, 1967) and, as detailed in the introduction, has subsequently been reported from 4 other species of darter throughout the center of the continent (Hanek and Fernando, 1971; Kritsky and Leiby, 1971; Molnar et al., 1974; Kozel and Whittaker, 1982; Dechtiar and Christie, 1988; Dechtiar et al., 1988). The original species description (Wellborn and Rogers, 1967) and the subsequent redescription (Kritsky and Leiby, 1971) present important features of the haptoral and penal sclerites (Figs. 16, 17). We supplement this information by providing a detailed lateral view of the marginal hook sickle (Fig. 18).

In addition to providing a key to known species of *Gyrodactylus* from darters, we have provided photographs of the marginal hook sickle of type species (Figs. 19–26). These types are deteriorating because they were originally mounted in glycerine jelly. In spite of the less than ideal quality of the photographs, it will be important for future studies to have some accurate record of their morphology.

Key to Known Species of *Gyrodactylus* from Darters

1. Anterolateral processes of ventral bar prominent, greater than 8 μm in length 2
   Anterolateral processes of ventral bar not prominent, less than 5 μm in length 4
2. Marginal hook sickle stout and compact and relatively short in length (6–7 μm) (Fig. 9) ..... *G. percinae*
   Marginal hook sickle delicate and 8.0–8.5 μm long 3
3. Marginal hook sickle with normally recurved point (Fig. 6) ..... *G. rafinesqueii*
   Marginal hook sickle with an open, only slightly recurved point (Fig. 12) ..... *G. bretinae*
4. Marginal hook sickle with short stout shaft (Fig. 18) ..... *G. etheostomae*
   Marginal hook sickle with long delicate shaft (Fig. 15) ..... *G. nigrum*

Species of *Gyrodactylus* that parasitize darters appear to be host-specific toward this group of fishes. This was evident in Russell Creek, where *G. rafinesqueii* sp. n. and *G. etheostomae* occurred only on darters and not on any of the 4 cyprinids that shared the habitat. Similarly, *G. rafinesqueii* sp. n. occurred on darters but did not occur on cyprinids in Marrowbone Creek. However, our samples indicate that the degree of host specificity varies with species of *Gyrodactylus*. *Gyrodactylus rafinesqueii* sp. n., for example, appears to be host-specific toward a group of closely related species (Page, 1981) that are collectively known as snubnose darters and assigned by various authors to one or another of 2 subgeneric names, *Nanostoma* (Page,



Figures 19–26. Photomicrographs of marginal hook sickles of type specimens of species of *Gyrodactylus* described from etheostomatini fishes. Scale bar = 10 μm. 19. *G. rafinesqueii* sp. n. Nomarski interference contrasts. 20. *G. percinae*, embryo (holotype USNPC 61027), Nomarski interference contrast. 21. *G. percinae* (holotype, phase contrast). 22. *G. bretinae* (holotype USNPC 61626). 23. *G. bretinae*, embryo (holotype). 24. *G. nigrum* (holotype USNPC 71232). 25. *G. etheostomae* (voucher specimens, USNPC 71659).

1981) or *Ulocentra* (Bailey and Etnier, 1988). Regardless of the controversy over the taxonomy of this group of fishes, we did not collect *G. rafinesqueii* sp. n. from any species other than those that are indisputably snubnose darters.

Gyrodactylus etheostomae appears to be less specific than *G. rafinesqueii* sp. n. In our samples, *G. etheostomae* parasitized 4 species of darters that are currently classified in 3 subgenera (*Oligocephalus*, *Doration*, and *Nanostoma*/*Ulocentra*; Page, 1981; Bailey and Etnier, 1988). *Gyrodactylus etheostomae* has previously been reported from 4 other species of darter and 2 additional subgenera, *Boleichthyes* and *Boleosoma* (Wellborn and Rogers, 1967; Kritsky and Leiby, 1971; Molnar et al., 1974).

The occurrence of *G. etheostomae* on *E. barrenense* at Trammel Fork may be interpreted as further evidence that this species is less host-specific than *G. rafinesqueii* sp. n., but more importantly it demonstrates that darters of the subgenus *Nanostoma*/*Ulocentra* can support populations of *Gyrodactylus* other than *G. rafinesqueii* sp. n. *Etheostoma barrenense* is unquestionably a sister species of *E. rafinesquei* (Page and Burr, 1982), the type host of *G. rafinesqueii* sp. n. However, *G. rafinesqueii* sp. n. was not collected at Trammel Fork. We cannot exclude the possibility that the occurrence of *G. etheostomae* on *E. barrenense* was incidental or transient. Nevertheless, *G. etheostomae* has a much broader host specificity than *G. rafinesqueii* sp. n.

The observed differences in host specificity are not the result of host-specific differences in habitat. All species of darters parasitized by *G. rafinesqueii* sp. n. have been collected with 1 or more of the species that are parasitized by *G. etheostomae* (Kuehne and Barbour, 1983; Page, 1983). Unpublished microhabitat data from our Russell Creek site indicate significant microhabitat overlaps among *E. bellum*, *E. caeruleum*, *E. rafinesquei*, and *E. stigmaeum*. The absence of gyrodactylids from darters of the subgenera *Catonotus* (*E. flavellare* at Russell Creek), *Nothonotus* (*E. bellum* at Russell Creek and *E. rufilineatum* at Marrowbone Creek), and *Etheostoma* (*E. blennioides* at Russell Creek and Marrowbone Creek) further supports the conclusion that host–parasite relationships are narrowly constrained.

It is tempting to conclude that the narrow host specificity of *G. rafinesqueii* sp. n. for snubnose darters is a result of coevolutionary history. However, the phylogeny of snubnose darters is significantly uncertain to allow such a conclusion. Additional sampling from sites where other species of snubnose darter occur syntopically with darters that are known hosts of *G. etheostomae* and with darters of the subgenus *Etheostoma* (see Bailey and Etnier [1988] and Page [1981] for a justification) should yield valuable information regarding the ecology of the parasites as well as the phylogeny of snubnose darters. That host-specificity among taxa of Monogenea can be used as taxonomic indicators in parasitized fishes has been recently demonstrated by Lambert and El Gharbi (1995).

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